台灣昆蟲 32: 139-153 (2012)
Formosan Entomol. 32: 139-153 (2012)

Stage-structured Population Growth of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae): a Simulation Approach

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ABSTRACT

The growth of a stage-structured population of *H. armigera* was simulated for four variable conditions. Age-stage specific growth rate, and fecundity obtained from an age-stage, two-sex life table analysis were used to project the population growth for 60 days, starting with an average pair of young adults representing the population. Because the survival rate and fecundity used for the population projection were collected from the whole population, initializing the simulation with a pair of average individuals is appropriate. The projection results obtained by using the total number of eggs and the number of eggs that hatched were compared. The population projection obtained by using the total number of eggs provided an erroneous projection of the population growth. The population growth increased the shorter the life cycle, in the following order: artificial diet at 29°C > artificial diet at 25°C > hybrid sweet corn > asparagus. The number of cumulative insect-days and weighted insect-days were also calculated. This study demonstrated the advantages of a computer simulation based on the age-stage, two-sex life table in revealing stage-structured population growth. This knowledge is critical for the timing of integrated pest management.

Key words: life table, insect-days, weighted stage size, simulation

Introduction

Helicoverpa armigera (Hübner) (Lepidoptera: Noctuidae) is one of the most notorious pests in agriculture. Integrated pest management strategies (IPM) for *H. armigera* have been proposed to suppress its population from reaching economically damaging levels (Kogan, 1998; Bajwa and Kogan, 2002; Prokopy and Kogan, 2003). For a rational IPM program, however, it is crucial to have a thorough understanding of the population ecology of the target pest. For most insect

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populations, stage differentiation and overlapping are important phenomena. These two critical aspects of insect population ecology are embedded in their demographics, and dictate the population dynamics. The characteristics of a pest population are emphasized by their demographics, particularly in relation to the patterns of population growth, survivorship, and reproduction, while population dynamics emphasize the causes and effects of these demographics (Price, 1997).

The patterns of population growth are a cornerstone for designing an ecologically sound pest management program; however, these patterns vary significantly based on food and environmental conditions. In this regard, knowledge of the stage structure of a pest population is necessary to facilitate the projection of population growth. Simulating the stage-specific population growth of a pest based on its life table characteristics can describe the population growth pattern under given conditions. Chi and Liu (1985) developed the age-stage, two-sex life table theory, which includes stage and sex differentiation and incorporates a variable developmental rate among individuals. Gutierrez (1996) highlighted the practical applications of life tables by including the age stage and two sexes in a life table construction. The age-stage, two-sex life table has been used in a considerable number of published and unpublished (theses and dissertations) studies. Some of the recent publications on this topics include Gao *et al.* (2012), Han *et al.* (2012), He *et al.* (2012), Huang and Chi (2012), Jha *et al.* (2012), Nguyen and Shih (2012), and Seyed-Talebi *et al.* (2012).

A life-table study provides two types of information: basic data and derived parameters (Farhadi *et al.*, 2011; Huang and Chi, 2012). The age-stage specific growth rate, age-stage specific developmental rate, age-stage specific survival rate and age-stage specific fecundity are the basic data that are calculated directly from the life history data of a cohort. These basic data are used to estimate derived parameters, such as the intrinsic rate of increase (r), finite rate of increase (λ), and mean generation time (T). The derived parameters are applicable only to a population with a stable age distribution, which is unlikely to occur under changing environmental conditions. Although the intrinsic rate of increase has frequently been used as an important parameter to evaluate the growth potential of insect populations under varying conditions, any projection based on this parameter will have limited applicability in pest management. Based on basic data, an age-stage, two-sex life table offers a way to simulate population growth for a month without assuming a stable age distribution (Chi and Liu, 1985). A simulation based on an age-stage, two-sex life table reveals the stage structures of both sexes in a pest population at any time (e.g., Chi, 1988, 1990; Tsai and Chi, 2007; Kavousi *et al.*, 2009; Farhadi *et al.*, 2011; Huang and Chi, 2012).

In the present study, the age-stage, two-sex life-table theory was applied to simulate the population growth of *H. armigera* based on its life table characteristics under four conditions. Population growth patterns under different food and environmental conditions showed the comparative fitness of an insect under a particular condition. In addition, population projections using the total number of eggs laid and the total number of eggs hatched were compared to accurately determine the biological characteristics of *H. armigera*. In this study, the term "hatched eggs" refers to the viable eggs that could hatch to first instars. The cumulative insect-days and weighted insect-days were also calculated and compared. This study demonstrates the advantages of an age-stage two-sex life table by revealing the stage and sex structure and for projecting population growth.

Materials and Methods

Helicoverpa armigera Colony

Initially, *H. armigera* larvae were collected from fields in Taichung County and maintained in the Microbial Control Laboratory, Department of Entomology, National Chung Hsing University Taichung, Taiwan to establish a founding colony of this pest. The colony was periodically supplemented with larvae collected from the field to reduce inbreeding depression. The colony was maintained on an artificial diet at 25°C. The composition of the artificial diet was modified from Kao (1995). The ingredients of this diet were as mentioned in Jha *et al.* (2012).

Host plant materials

Hybrid sweet corn (*Zea mays*) and asparagus (*Asparagus officinalis*) were used as the plant materials in this study for feeding *H. armigera*. Cobs of the KY bright jean, a variety of hybrid super sweet corn were obtained from plants grown in a pesticide-free field, stored in a deep freezer at -20°C and supplied to *H. armigera* as food after defrosting. Asparagus (*Asparagus officinalis*) foliage was also obtained from plants grown in a pesticide-free field. A batch of healthy young asparagus foliage was collected from the field every 2-3 days during the experiment. The lateral branches were excised, and the stem portion of the excised branches was dipped into water to protect the foliage from drying. The foliage was provided to *H. armigera* as food.

Life-table study

The life tables of *H. armigera* were studied in the laboratory by rearing the insects at 25°C on an artificial diet, a hybrid sweet corn diet, and an asparagus diet, and at 29°C on an artificial diet. A colony of *H. armigera* was reared on these respective diets and temperatures for one generation in a growth chamber at 65 ± 5% RH and a photoperiod of 14:10 (L:D) prior to the life-table study. Newly emerged adults were paired and then kept in pairs in an individual oviposition container (a plastic cup measuring 9 cm in diameter × 5.5 cm in high, and lined with paper towel). The adults were provided daily with a cotton ball soaked in 30% honey solution. The eggs from each female were collected in Petri dishes (9 cm in diameter) and kept separately in a growth chamber as mentioned above. The hatching rate was observed daily. Due to the variable hatching rate of eggs laid by females of different ages, we used the hatched first instars with a known egg duration to begin the life table study. This way we excluded the egg mortality, and all eggs used in the simulation were hatchable. The procedure of Jha *et al.* (2012) was followed in this study. The survival and fecundity were recorded daily for each individual until death. The eggs laid by each female at a different age were collected and kept separately to record the hatching rates. Based on the theory of the age-stage, two-sex life table (Chi and Liu, 1985) and the method described by Chi (1988), the raw data were analyzed by using the user-friendly computer program, TWOSEX-MSChart (Chi, 2010), which is available at http://140.120.197.173/Ecology/prod02.html (National Chung Hsing University, Taichung, Taiwan) and http://nhsbig.inhs.uiuc.edu/wes/chi.html (Illinois Natural History Survey).

Population Projection

The analytical results of the age-stage, two-sex life table include the *G, D* and *F* matrices and the operation of these matrices can project the age-stage structure of a pest population at time $t + 1$:

$$N_t \xrightarrow{G,D,F} N_{t+1} \qquad (1)$$

Element g_{xj} of the age-stage-specific growth rate matrix (G) is the probability that an individual of age x and stage j will grow to age $x + 1$ but will remain in stage j

Table 1. Age of the female and male adults of the initial population used in the simulations

Rearing Condition	Age (days)	
	Female	Male
Artificial diet 29°C	26	26
Artificial diet 25°C	31	31
Hybrid sweet corn 25°C	36	36
Asparagus 25°C	40	41

after one age unit. Element d_{xj} of age-stage-specific development rate matrix (D) is the probability that an individual of age x and stage j will survive and develop to age $x + 1$ and stage $j + 1$, respectively. In the age-stage-specific fecundity matrix (F), f_{xj} is the number of offspring produced by an individual in age x and stage j. The detailed calculation procedures are discussed in Chi and Liu (1985). Beginning with an initial population with a designated age structure (Table 1), this projection simulates the growth of a population based on the age-stage growth rate, developmental rate, and fecundity under unlimited conditions. The designated age in Table 1 is counted from the egg stage and indexed from 0. Because the potential of a pest population to damage plants varies according to the stage-specific consumption rate, we assigned a weighting coefficient (w_j) to each stage based on its consumption rate when reared on asparagus (unpublished data) (Table 2). Because only the larvae cause damage to plants, the weighting coefficients for the other stages were set to zero (Table 2). The weighting coefficient of a specific larval instar was calculated as follows:

$$w_j = \frac{c_j}{c_h} \quad (2)$$

where c_j is the consumption of stage j, and c_h is the highest level of consumption. Because the fifth-seventh instar has the highest consumption rate, w_6 is equal to unity. The weighted size of the *H. armigera* population on day t was then calculated as follows (Chi, 1990):

Table 2. Stage-specific weighting coefficients used in the simulations

Serial stage code (j)	Stage	Weighting coefficient
1	Egg	0
2	First instar	0.005
3	Second instar	0.007
4	Third instar	0.019
5	Fourth instar	0.050
6	Fifth-seventh instar	1
7	Prepupa	0
8	Pupa	0
9	Female	0
10	Male	0

$$n_w(t) = \sum\sum n_{xj}(t) \cdot w_j \quad (3)$$

Insect-days are the summation of the number of pests over the number of days that they survive and cause damage to a crop. Insect-days should be used as an index of crop damage (Ruppel, 1983). When an age-stage, two-sex life table is used, the cumulative insect-days ($CumSD$) and weighted cumulative insect-days generate a more rational index of the overall damage caused by a pest population because it takes into consideration both sexes, the variable developmental rate among individuals, and the stage-specific consumption rate. According to Chi (1990), these indices can be calculated as follows:

$$CumSD = \sum_{t=0}^{T}\sum_{j=2}^{6} n_{xj}(t) \quad (4)$$

$$CumWSD = \sum_{t=0}^{T}\left[\sum_{j=2}^{6}\left(\sum n_{xj}(t) \cdot w_j\right)\right] \quad (5)$$

where T is the duration of the crop growing season, and $j = 2$ to 6 are the stages that cause damage (Table 2). The program TIMING-MSChart (Chi, 2012) used for these simulations is available from the above-mentioned websites.

Results

The population growth rates of *H. armigera* reared at 25°C on an artificial diet, a hybrid sweet corn diet, or an asparagus diet, and at 29°C on an artificial diet were projected and compared with each other. Starting with an initial population of one pair of the youngest adults, the population growth was simulated for 60 days (Figs. 1-4). Because the survival rate and fecundity used in population projection were calculated from the whole population, the starting pair could properly represent the population. The resulting figures revealed the change in the age-stage structure of *H. armigera* under the given conditions. The larval populations under these four conditions are shown in Fig. 5. The weighted stage sizes are also depicted in Fig. 6 to show the damaging potential of the pest population.

In each figure, significant differences between the simulations based on the number of eggs laid and the number of hatched eggs can be observed. The simulation based on the total number of eggs generated higher curves for each stage than did the simulation based on the number of hatched eggs. Moreover, the curves were wider and peaked later in most of the simulations based on the total number of eggs. For example, in the simulation based on the total number of eggs, the peaks for the first and second larval cycles were approximately 4- and 18-fold greater, respectively, than those produced in the simulation based on the number of hatched eggs (Fig. 1). Similarly, the first peak of the larval stage occurred 3 days later than the peak in the simulation based on the number of hatched eggs, and the second peak was more than 6 days later (Fig. 1). Moreover, the duration of the egg stage was 6 days shorter in the simulation based on the number of hatched eggs compared to the simulation based on the total number of eggs (Fig. 1). These results show that the simulation based on the total number of eggs resulted in an erroneous projection of population growth that could lead to making the wrong decision.

The growth curves of the larval stage in Fig. 5 were compiled for making a comparison. The simulation curves based on the weighted stage size using the number of hatched eggs represent the damage potential of *H. armigera* under respective scenarios (Fig. 6). Due to a faster development, the curve of the weighted insect-days for an artificial diet at 29°C had the lowest amplitude, the shortest period, and the fastest oscillation compared to the other curves. In contrast, due to a slower development, the weighted insect-days curve for asparagus at 25°C had the highest amplitude and the slowest oscillation compared to the other curves. At 29°C, the weighted insect-days curve started to rise again after only 40 days. Thus, the height of the asparagus curve at the day 60 was the lowest, despite being the highest at day 30. This result shows that the *H. armigera* population grew slowly on asparagus during the first 40 days, but the intensity of the damage was relatively high. The total damage at 29°C after 60 days was the highest (Fig. 6). All of these details can only be observed by using a computer simulation based on the age-stage, two-sex life table.

The values of the total cumulative insect-days and weighted insect-days corresponding to the population curves are given in Table 3. Under all tested conditions, the simulation based on the number of hatched eggs resulted in a lower number of cumulative stage-days and weighted insect-days than the simulation

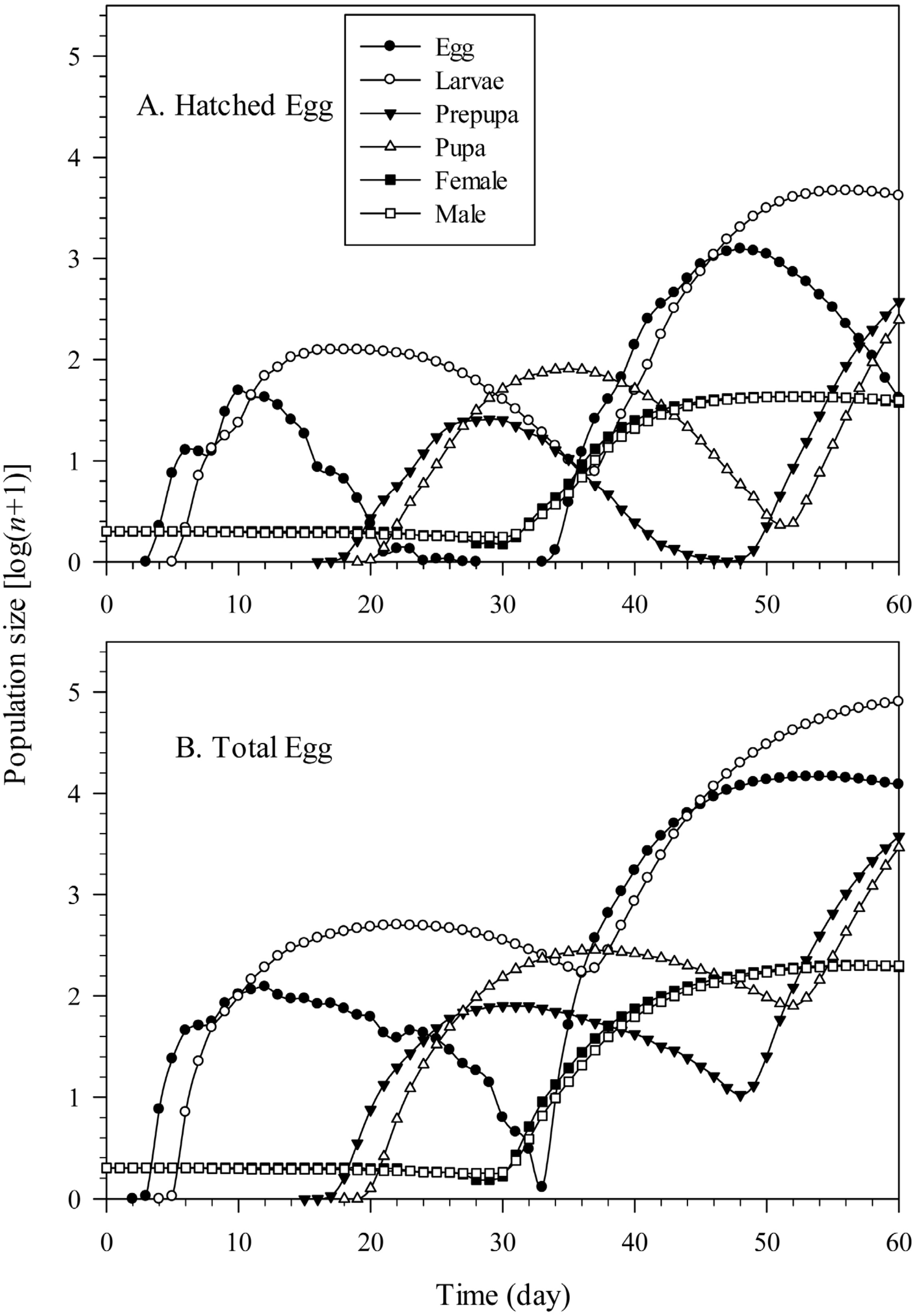

Fig. 1. Population projections of *Helicoverpa armigera* reared at 29°C on an artificial diet using the hatched eggs (A) and the total number of eggs (B).

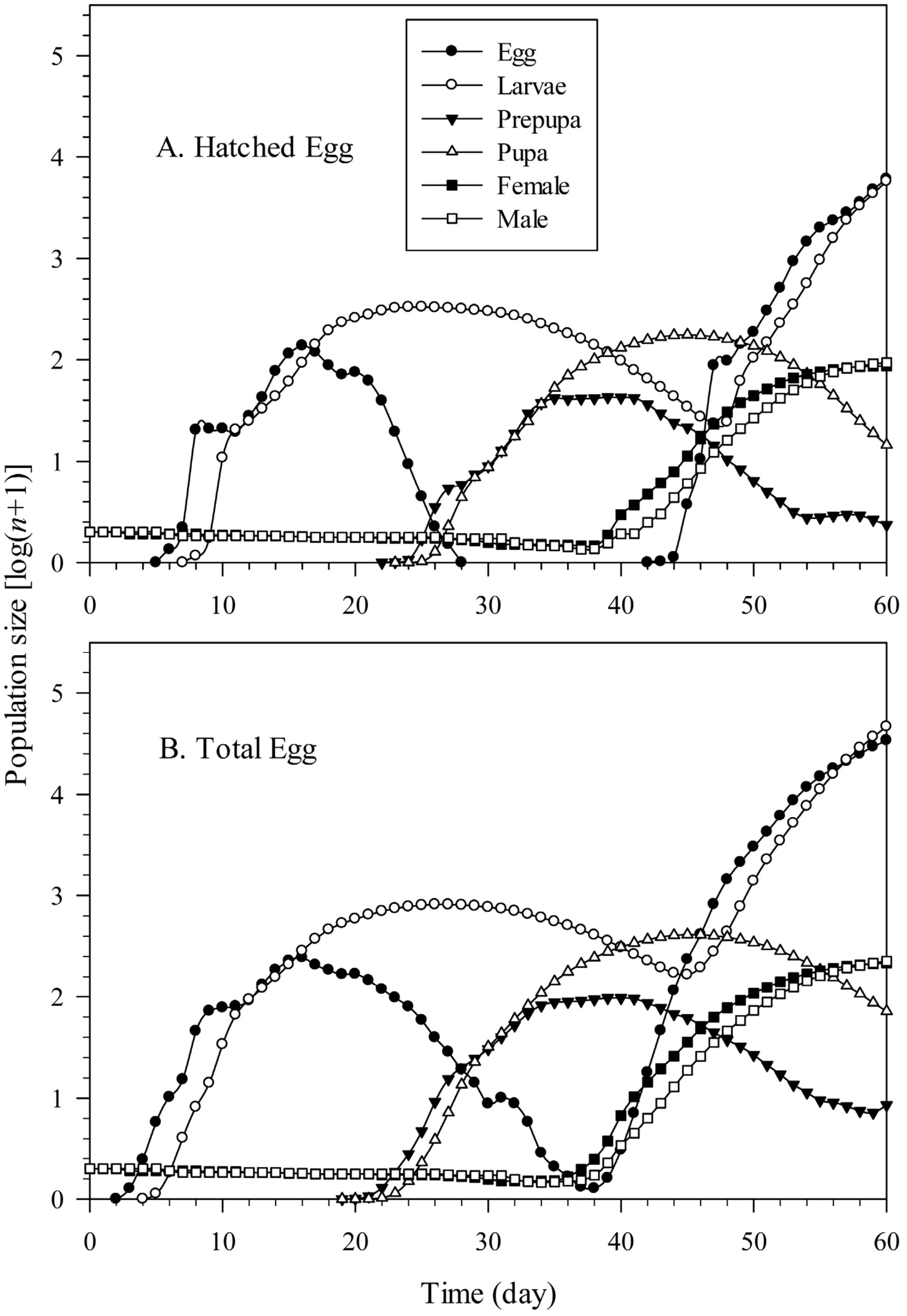

Fig. 2. Population projections of *Helicoverpa armigera* reared at 25°C on an artificial diet using the hatched eggs (A) and the total number of eggs (B).

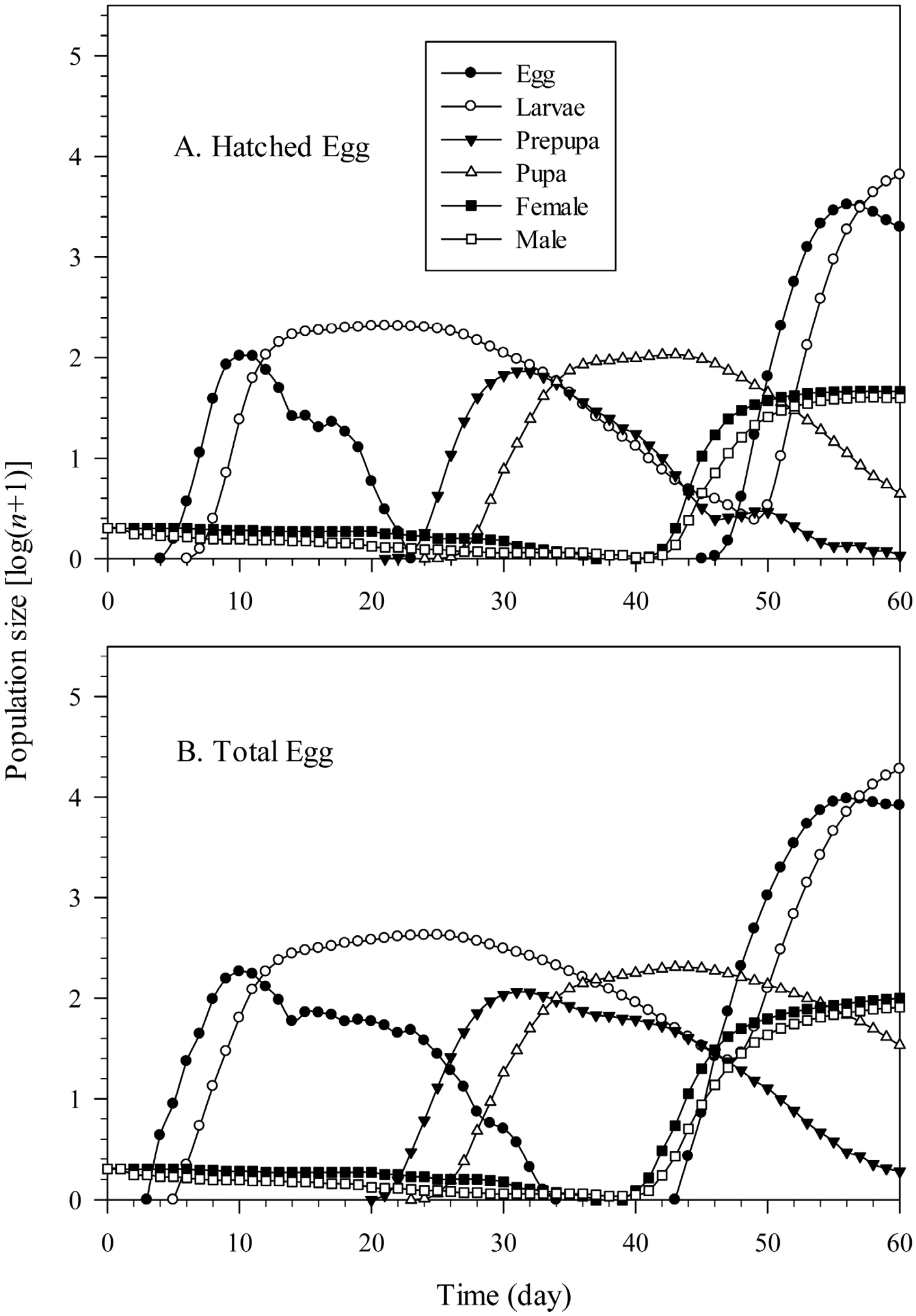

Fig. 3. Population projections of *Helicoverpa armigera* reared at 25°C on hybrid sweet corn using the hatched eggs (A) and the total number of eggs (B).

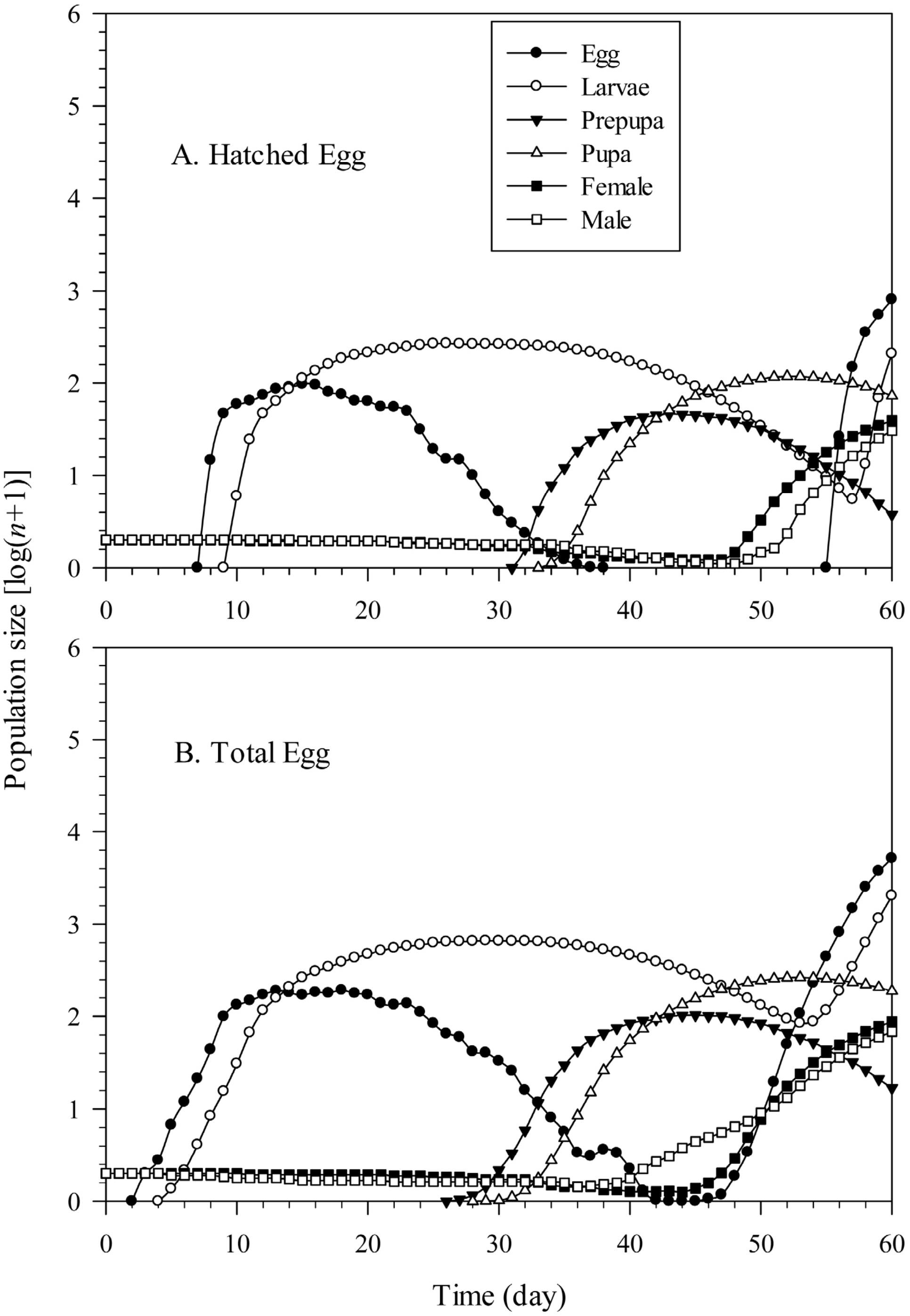

Fig. 4. Population projections of *Helicoverpa armigera* reared at 25°C on asparagus using the hatched eggs (A) and the total number of eggs (B).

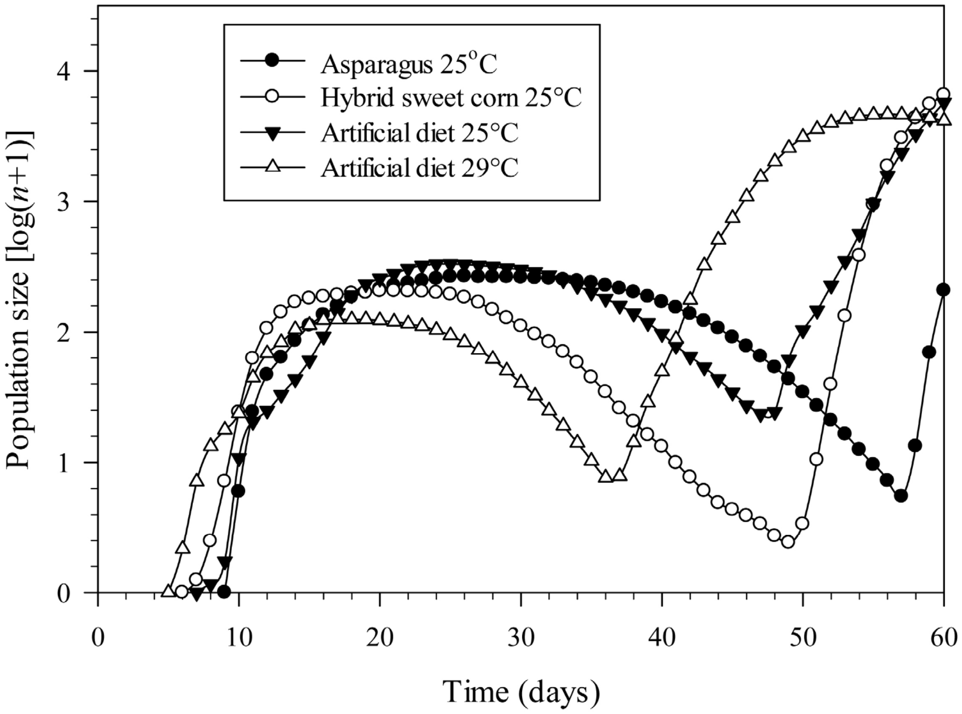

Fig. 5. Larval growth projections of *Helicoverpa armigera* under four different scenarios.

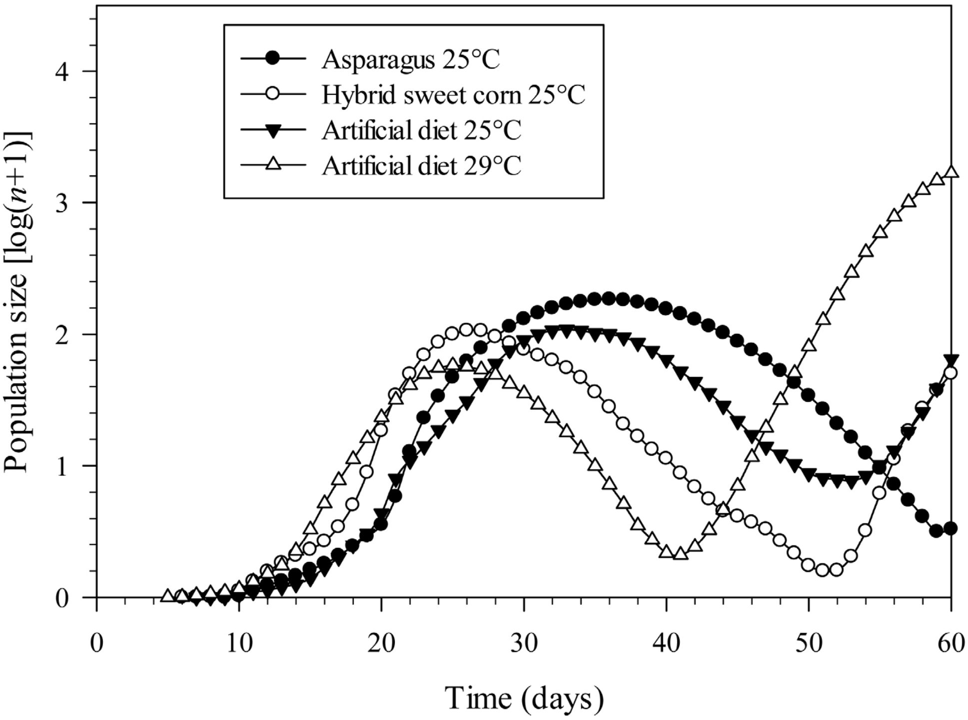

Fig. 6. Weighted population growths of *Helicoverpa armigera* under four different scenarios.

Table 3. Cumulative insect-days and weighted insect-days of each simulation result

Rearing Condition	Insect-days			
	Hatched eggs		Total eggs	
	Cumulative	Weighted	Cumulative	Weighted
Artificial diet 29°C	57,604	8,598	736,319	85,437
Artificial diet 25°C	26,239	1,736	199,407	6,170
Hybrid sweet corn 25°C	26,779	1,368	84,471	3,468
Asparagus 25°C	7,248	3,220	22,252	8,291

based on total eggs. The total number of cumulative insect-days was the lowest for asparagus, while the number of weighted stage days was the lowest for hybrid sweet corn. Compared to the other conditions, the artificial diet at 29°C resulted in the greatest number of insect-days and weighted insect-days.

Discussion

Helicoverpa armigera is a holometabolous insect with four clearly distinguishable life stages: egg, larva, pupa and adult. The hatchability of the eggs varies with maternal age. The larval stage undergoes 5 to 7 molts, depending on the food and environmental conditions (Fitt, 1989; Casimero *et al.*, 2000). The growth, development, and consumption rates vary among individuals in a cohort. The offspring sex ratio also varies with maternal age. These fascinating biological variations, also reported in Jha *et al.* (2012), affect the demography of this insect and create complications in evaluating its fitness and damage potential under different conditions. The intrinsic rate of increase is considered to be the most useful and appropriate life-table parameter for comparing the fitness of populations across diverse climatic and food-related conditions (Southwood, 1966; Smith, 1991; Kingsolver and Huey, 2008). However, the intrinsic rate of increase (r) is only applicable to a population with a stable age distribution, while survival rate and fecundity can be applicable to contemporary population. Thus, a population projection based on an age-stage-specific survival rate and an age-stage-specific fecundity rate provides a more realistic and reliable insight into the population's ecological fitness and damage potential. In this regard, an age-stage, two-sex life table facilitates a proper way to simulate population growth with stage differentiation.

Based on the age-stage, two-sex life table theory, a population projection can reveal the short-term growth of a pest population by depicting the stage structure. This theory has also been applied to the timing of pest management (Chi, 1990). The advantage of taking the male population and variable development into account is that a population growth simulation using an age-stage two-sex life table reveals overlaps in the stage curves (Figs. 1-4). On the other hand, ignoring the male population and variable development results in inaccurate simulations and generates a single curve representing the total female population.

Despite the lower fecundity observed at 29°C, the population grew faster than at 25°C. This result is due to the shorter developmental duration of each stage at 29°C. Similarly, the growth of the population reared on hybrid sweet corn was faster than the population reared on asparagus. The order of population growth was as follows: artificial diet at 29°C > artificial diet at 25°C > hybrid sweet corn diet > asparagus diet. The intrinsic rate of increase calculated for these conditions followed the same order.

The insect-day proposed by Ruppel (1983) is an index of arthropod abundance over time; it can be used to estimate damage potential. Due to the difficulties of computer simulation and life table theory, the insect-day did not gain as much attention as it deserved. It is particularly useful when yield loss results from an accumulation of feeding injury over time (Rhainds *et al.*, 2010). The simulation of population growth based on weighed stage size in combination with insect-day techniques enables us to assess the damage potential under given conditions and incorporate the damage potential estimate in integrated pest management. For example, despite the relatively high cumulative insect-day values for hybrid sweet corn, the higher weighted insect-day value was obtained for asparagus (Table 3). This higher value resulted from the joint effect of two distinct phenomena: a longer larval duration due to slower development (i.e., a longer feeding period and more larval instars) and more larvae due to higher fecundity on asparagus.

The computer simulation of population growth based on life- table data is a useful, comprehensive, and efficient technique for predicting and comparing the growth of populations. Although our simulation is limited to four conditions, this study demonstrated that this technique can be applied to compare the growth of populations across diverse climatic and food-related conditions when survival rate and fecundity data are known. In addition, understanding the growth characteristics of a pest population under different conditions can lead to better management decisions. This study demonstrated that because the age-stage, two-sex life table takes the variable developmental time, stage differentiation, and both sexes into consideration it has the advantages of revealing stage-structured population growth in a manner relevant to IPM. Because insect life tables vary significantly with food (Jha *et al.*, 2012), temperature (Atlihan and Chi, 2008), and other environmental factors (Yin *et al.*, 2009), precisely projecting populations in the field is a difficult task (Huang and Chi, 2012). Despite its difficulties, entomologists should not discount the life table. Indeed, more efforts and studies are needed to make IPM a possible task that is truly based on ecology.

Acknowledgments

We thank Prof. Dr. S. J. Tuan and Dr. C. F. Lai for their support in conducting this study. This project is supported by NSC 98-2313-B-005-020-MY3 and 99AS-5. 3.1-ST-aG.

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Received: May 28, 2012
Accepted: June 13, 2012

利用玉米穗蟲 ***Helicoverpa armigera* (Hübner)** 的齡期結構進行族群模擬

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摘　　要

本試驗在四種不同的條件下模擬玉米穗蟲 *Helicoverpa armigera* (Hübner) 含齡期結構的族群增長。利用年齡齡期兩性生命表實驗所蒐集的生長及繁殖數據，以初羽化之單對雌雄為起始族群，模擬 60 天的族群增長。由於存活率及繁殖率的資料是由整體族群所得，利用單對初羽化雌雄作為起始，可模擬族群增長。本文比較以總卵數及實際孵化卵數模擬之結果。以總卵數進行族群模擬而忽略孵化率的差異會造成錯誤模擬結果。生活史越短在族群增長的速度上會越快，四種不同條件的族群增長速度依序為：在 29°C 下人工飼料 > 25°C 下人工飼料 > 雜交甜玉米 > 蘆筍。我們也計算累積的昆蟲日 (insect-day) 及加權的昆蟲日。本文證實使用年齡齡期兩性生命表在族群模擬上的優點。這些知識對預測綜合害蟲防治時機是非常重要的。

關鍵詞：生命表、每天的昆蟲量、加權昆蟲量、模擬。

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